

# Spatial Distribution of Three Species of Bivalves on an Intertidal Flat: the Interaction of Life-history Strategy with Predation and Disturbance

by

MARK L. BOTTON

Excel Division, Fordham University, College at Lincoln Center, New York, New York 10023

*Abstract.* Spatial distributions of three species of bivalves, *Gemma gemma*, *Mulinia lateralis*, and *Mya arenaria*, were examined on a Delaware Bay intertidal flat inhabited by large numbers of horseshoe crabs, *Limulus polyphemus*. Populations within and outside of predator exclosures were compared. *Gemma gemma*, which has no actively swimming larval stage, was strongly aggregated after settlement. Larger individuals in protected plots remained aggregated, but in unprotected plots, there was some tendency toward randomization. *Mulinia lateralis*, which has planktonic larvae and actively burrowing juveniles, was most aggregated just after settlement. Protected individuals of *M. lateralis* were much more numerous, and were less aggregated, than unprotected *M. lateralis*. *Mya arenaria* also has a planktonic larval stage, but juveniles are somewhat less motile. Protected individuals were initially aggregated and remained so; predators eliminated nearly all unprotected *M. arenaria*.

## INTRODUCTION

KNOWLEDGE OF THE spatial distribution of organisms is important to expedient sampling, and spatial patterns may also provide information on inter- or intra-specific relationships. Clumping or aggregation must be considered in designing a sampling strategy (GAGE & GEEKIE, 1973; MOORE & McLAUGHLIN, 1978; BOTTON, 1979; DOWNING, 1979). Spatial patterns may reflect physical variability in substratum, or be indicative of biological interactions. For example, spatial pattern in spionid polychaetes and its relationship to aggressive behavior was reported by LEVIN (1981).

Life-history strategies may influence spatial distributions of bivalves (BRADLEY & COOKE, 1959; MATTHIESSEN, 1960; JACKSON, 1968; GREEN & HOBSON, 1970; THOMPSON, 1982). Juveniles of species that brood larvae, such as *Gemma gemma*, may be aggregated (JACKSON, 1968; THOMPSON, 1982), as with a "seed shadow" about a parent tree. The spatial pattern of species with planktonic larvae is difficult to predict; hydrographic factors such as water temperature and salinity may influence the dispersion of larvae prior to metamorphosis, and conditions of the settlement surface, including the presence of predators, are also significant (THORSON, 1966; WOODIN, 1976). After settlement, waves and currents may redistribute bivalves (MATTHIESSEN, 1960; JACKSON, 1968; THOMPSON, 1982).

Predation may also influence the spatial distribution of bivalves. In theory in a heterogeneous environment, predators should concentrate their feeding in the richest patches, and remain until their net rate of energy intake in these patches falls to the average value for the habitat (HUGHES, 1980; SIH, 1982). Such "optimal patch use" predators should therefore equalize prey density among patches.

A caging study that excludes predators is a straightforward approach to studying the effect of predation on spatial distribution of bivalves within comparably sized caged and uncaged plots. SCHNEIDER (1978) found that shorebirds equalized the spatial dispersion of the prey on a Massachusetts mudflat. The present paper describes a cage study conducted on intertidal sand flats in Delaware Bay, New Jersey, in the spring-summer of 1978 and 1979. Population censuses of the horseshoe crab, *Limulus polyphemus* (Linnaeus) (BOTTON, 1984), and bird-exclosure treatments (BOTTON, 1983) strongly suggested that the principal predator and sediment disturber was *L. polyphemus*, which utilizes these beaches for several months for reproduction. Effects of caging on the abundance and size-frequency distributions of bivalves are considered in another paper (BOTTON, 1984). Here, I consider the influences of life histories, predation, and disturbance on the spatial patterns of the three most abundant species of infaunal bivalves, two with planktonic larvae—*Mya arenaria* Linnaeus, 1758 (Myacidae) and *Mulinia lateralis*

Table 1

Mean ( $\bar{x}$ ) and Coefficient of Dispersion (CD) for the three most abundant bivalve species in the 1978 predator enclosure experiments, using 2 enclosures. \* indicates aggregated distribution, based on the statistical procedure of CLARKE & MILNE (1955); otherwise, the distribution is random. Each mean and CD is based on 3 replicate 0.0048-m<sup>2</sup> cores.

Species	Date	Enclosure 1		Enclosure 2		Unprotected 1		Unprotected 2	
		$\bar{x}$	CD	$\bar{x}$	CD	$\bar{x}$	CD	$\bar{x}$	CD
<i>Mya</i>	6/8	12.3	0.9	8.0	5.3*	10.0	5.3*	1.7	3.3
	6/23	31.3	7.6*	19.3	3.5*	9.3	5.2*	5.7	1.1
	7/7	110.3	30.3*	44.0	4.1*	3.3	1.9	4.0	0.5
	7/20	42.0	3.9*	24.3	7.2*	0.0	—	1.3	0.2
	8/4	36.7	8.9*	25.7	1.7	0.7	0.3	0.3	0.7
<i>Mulinia</i>	6/8	48.7	2.3	86.0	19.2*	35.3	9.2*	33.0	12.2*
	6/23	142.7	35.2*	168.3	72.5*	60.0	21.6*	82.3	5.6*
	7/7	90.7	0.6	96.0	12.1*	59.3	17.2*	68.0	4.1*
	7/20	73.3	3.1	83.3	0.1	17.3	0.9	50.0	4.3*
	8/4	60.3	2.8	96.7	0.8	39.3	16.1*	18.3	0.6
<i>Gemma</i>	6/8	169.3	20.5*	77.7	21.4*	100.3	27.8*	24.7	7.6*
	6/23	100.7	9.7*	74.3	30.5*	31.7	7.7*	18.0	6.7*
	7/7	110.0	5.6*	96.3	51.6*	22.0	2.8	44.0	7.7*
	7/20	92.3	2.1	75.7	1.0	11.7	14.4*	19.3	2.1
	8/4	56.3	5.1*	37.3	0.8	13.3	2.2	15.7	3.9*

Linear regressions of Coefficient of Dispersion (y) on Mean (x):

Species	Intercept	Slope	r <sup>2</sup>
<i>Mya</i>	0.86	0.23	0.810
<i>Mulinia</i>			
All data	-9.49	3.06	0.467
Less 2 highest	7.30	0.001	0.0003
<i>Gemma</i>	3.35	0.14	0.209

(Say, 1822) (Mactridae)—and one with direct development—*Gemma gemma* (Totten, 1834) (Veneridae).

## MATERIALS AND METHODS

Field work was performed at the New Jersey Oyster Research Laboratory on the Cape May shore of Delaware Bay. Predator enclosures were 1.2 × 1.2 × 0.3 m wooden frames covered top and sides with large mesh wire (5.1 cm hexagonal openings in 1978, or 5.0 × 10.0 cm rectangular openings in 1979) to exclude shorebirds, large crabs, and fishes. The medium sand sediment (mean grain size = 0.38 mm, with <1% silt-clay) was not significantly altered by the cage (BOTTON, 1982).

To sample a cage, a 6-by-6 grid was painted on the side of the frame, and the location of a core was determined by rolling two dice. In 1978, three cores were taken from each of the two enclosures and three more from each adjoining unprotected plot on 8 June, 23 June, 7 July, 20 July, and 4 August. In 1979, four cores were taken from each of the three enclosures and from each unprotected plot on 16 April, 24 May, 14 June, 6 July, 20 July, and 3 August. Each cage plus its unprotected plot is hereafter referred to as a "site"; a distance of about 30 m separated the sites. Cores were taken with a glass jar, 7.8-

cm inside diameter (=0.0048 m<sup>2</sup>), which sampled to a depth of 10 cm. This core size was chosen because (1) the requisite number of replicates could be obtained without disrupting adjacent sediments or re-sampling a previous coordinate within the cage, and (2) prior qualitative sampling had revealed the small sizes and high densities of the infauna (see DOWNING [1979] on the relationship between benthos density, size of sampling devices, and number of replicates). Cores were washed through a 500- $\mu$ m mesh sieve, and the material retained was fixed in 10% formalin and transferred to 70% ethanol with rose bengal stain. Bivalves were enumerated and measured to the nearest 0.1 mm with an ocular micrometer or vernier caliper.

The spatial distribution of bivalve populations within sites was computed by the Coefficient of Dispersion (CD), which is the variance/mean ratio. This measure is based on the principle that for randomly distributed individuals, the mean number of individuals per core should equal the variance (Pielou, 1969). A CD significantly above one indicates that the population is aggregated, and values significantly less than one indicate a uniform dispersion. Statistical significance was based on the test of CLARKE & MILNE (1955), namely, a CD exceeding the confidence interval  $1 + 2\sqrt{(2n)/(n-1)}$ , where n is the number of



replicate cores used to sample each caged or uncaged plot. Bivalves with a CD within this boundary are considered to be randomly distributed.

## RESULTS

In 1978, caged sediments contained a significantly higher density of individuals than uncaged sediments. This response resulted from the enhanced survival of the bivalves *Mya arenaria*, *Mulinia lateralis*, and *Gemma gemma* (Table 1, and BOTTON, 1984).

*Mya arenaria* was generally aggregated in cages, but randomly dispersed in uncaged sediments. Only the 1978 year-class was present on 8 June, based on the size-frequency distribution which showed a mean shell length less than 2 mm, with no individuals > 5 mm (BOTTON, 1984). The spatial pattern of newly set *M. arenaria* was similar regardless of treatment (Table 1). From 23 June onward, *M. arenaria* was aggregated in all caged sediments, except for enclosure 2 on 4 August. In contrast, the few *Mya* surviving in unprotected sediments during July and August were randomly distributed. Pooling both caged and uncaged samples, most of the variability in the Coefficient of Dispersion was related to the mean (linear regression,  $r^2 = 0.81$ ; Table 1).

*Mulinia lateralis* was even more abundant than *Mya arenaria*, but did not show the same spatial pattern. Only the 1978 year-class of *Mulinia lateralis* was present; when first sampled (8 June), mean shell length was 1.5 mm, and there were no individuals above 3 mm in length (BOTTON, 1984). On 8 June, the day that cages were put in place, *M. lateralis* was highly aggregated in three of the four areas (Table 1). On 23 June, caged individuals of *M. lateralis* were aggregated; on 7 July, only cage 2 was aggregated, but on 20 July and 4 August, all caged *M. lateralis* were randomly distributed. The responses of the uncaged areas were not consistent. Overall, excluding 8 June, *M. lateralis* was aggregated in 6 of 8 uncaged samplings, but only 3 of 8 caged samplings. There was a weak positive relationship between CD and mean, as shown by linear regression. When all data were considered,  $r^2$  was 0.47; however, when the two highest means (168.3 and 142.7 individuals/core) were eliminated,  $r^2$  was only 0.0003 (Table 1).

The spatial distribution of *Gemma gemma* was analyzed in two ways: (1) the population as a whole, *i.e.*, by combining all size classes (Table 1), and (2) separate analysis of new recruits (<1.4 mm) and older individuals (>2.8 mm) (Table 2). In the first case, individuals of *G. gemma* from both caged and uncaged sediments were most aggregated early in the summer, *i.e.*, when clams were smaller and more numerous. Only 21% of the variability in CD was related to the population size (Table 1). The spatial distribution of new set was most aggregated early in the summer (Table 2). Larger *G. gemma* showed a mixture of clumped and random distributions, regardless of treatment.

The results from 1979 were limited to *Gemma gemma*, because both *Mya arenaria* and *Mulinia lateralis* had nearly complete recruitment failures (BOTTON, 1984). On 16 April, there were few small *G. gemma*, as the population consisted mainly of survivors from the 1978 year-class (Table 2, and BOTTON, 1984). Large numbers of the 1979 year-class were retained on a 500- $\mu$ m sieve from 14 June onward, and small individuals of *G. gemma* were generally aggregated in both protected and unprotected sediments. Large *G. gemma* individuals in unprotected sediments were randomly distributed in 15 of 18 instances (Table 2). In contrast, protected large *G. gemma* individuals were clumped in 12 of 17 cases.

The mean coefficient of dispersal for small *Gemma gemma* was 15.05 and for large *G. gemma*, 6.05. Protected clams were more aggregated (mean CD = 14.51) than unprotected clams (mean CD = 6.82) (Analysis of Variance,  $F = 6.85$ , 1,5 df,  $P < 0.05$ ).

## DISCUSSION

Aggregation, as measured by the coefficient of dispersion (variance/mean ratio), varies with mean density (DOWNING, 1979), but not all the variability in CD can be explained by this alone; biological factors must be considered. The three species studied have important life-history differences with respect to reproductive mode, mobility, and vulnerability to predation and sediment disturbance (Table 3). *Gemma gemma*, which has direct development, may be considered as an "equilibrium" species, somewhat resistant to predation (SCHNEIDER, 1978; WOODIN, 1981). *Mulinia lateralis* and *Mya arenaria*, which recruit by planktonic larvae, are "opportunists," quite vulnerable to predation (VIRNSTEIN, 1977; BOTTON, 1984).

The clumped distribution of small *Gemma gemma* found in 1979 and the first month of 1978 is consistent with JACKSON (1968). Older individuals of *G. gemma* were randomly distributed in the unprotected areas in the 1979 study, in agreement with JACKSON (1968) and GREEN & HOBSON (1970), though THOMPSON (1982) found that most *G. gemma* adults (defined as >0.9 mm length) on a San Francisco Bay mudflat were aggregated. The aggregation of larger *G. gemma* within enclosures may be imposed by the clumping of newly released juveniles, and retained in the absence of predation or sediment disturbance. The Delaware Bay intertidal flats are unstable and are reworked by horseshoe crab burrowing; thus, individuals of *G. gemma* are unlikely to remain in the vicinity where they set. Yet, the clumped distribution of unprotected <1.4 mm animals throughout 1979 suggests that either disturbance did not completely randomize the spatial pattern, or that continued release of juveniles overshadowed the impact of disturbance. The importance of predation to larger *G. gemma* is debatable, since several studies indicate that this species is not preferred prey to certain shorebirds (SCHNEIDER, 1978), crabs (WOODIN, 1981), or horseshoe crabs (BOTTON, 1982), whereas GREEN & HOBSON (1970)

Table 2

Spatial distribution of newly recruited (<1.4 mm) and older (>2.8 mm) *Gemma gemma* in the 1978 experiment (2 exclosures) and 1979 experiment (3 exclosures). CD = coefficient of dispersion; \* indicates aggregated dispersion. Each mean and CD in 1978 was based on 3 replicate 0.0048-m<sup>2</sup> cores; 4 replicates were used in 1979. Sites 1 and 2 in 1978 were not the exact same location as 1979.

Date	<1.4 mm clams				>2.8 mm clams			
	Protected		Unprotected		Protected		Unprotected	
	Mean	CD	Mean	CD	Mean	CD	Mean	CD
8 June 1978								
Site 1	58.0	7.1*	44.3	15.0*	0.0	—	0.3	0.7
Site 2	30.0	7.0*	13.3	4.5*	0.0	—	0.0	—
23 June 1978								
Site 1	6.7	2.2	1.3	0.7	9.7	0.6	1.0	0.7
Site 2	4.7	3.6	1.0	0.0	0.7	1.3	0.3	0.7
7 July 1978								
Site 1	3.3	1.1	1.3	0.2	66.0	7.8*	7.0	1.2
Site 2	5.3	1.3	6.0	1.3	39.7	27.9*	9.3	4.6*
20 July 1978								
Site 1	3.7	0.1	1.3	2.7	77.3	3.6	5.3	7.0*
Site 2	4.7	0.9	4.7	0.6	58.7	0.6	8.3	2.0
4 August 1978								
Site 1	1.3	1.2	3.7	0.4	49.0	5.4*	3.7	0.1
Site 2	6.3	3.2	4.3	1.4	27.0	1.3	5.7	2.5
16 April 1979								
Site 1	0.3	1.0	0.3	1.0	4.5	1.3	5.5	2.5
Site 2	0.8	1.2	0.3	1.0	7.3	2.5	5.5	1.0
Site 3	0.3	1.0	0.5	0.7	2.3	0.7	6.0	1.8
24 May 1979								
Site 1	0.5	2.0	2.0	2.0	9.8	7.1*	2.5	0.7
Site 2	4.8	14.2*	7.8	17.2*	9.3	25.0*	4.5	1.6
Site 3	2.8	3.7*	1.3	1.3	3.8	3.5*	1.5	1.1
14 June 1979								
Site 1	2.5	0.7	6.5	4.6*	4.0	0.7	3.8	2.9*
Site 2	35.0	105.2*	12.8	14.7*	14.3	10.1*	3.5	2.4
Site 3	18.5	11.3	2.8	2.0	14.5	20.3*	2.5	1.7
6 July 1979								
Site 1	8.0	4.6*	13.5	1.5	6.0	1.9	5.5	1.3
Site 2	50.3	14.0*	27.3	10.7*	25.3	20.3*	7.0	1.6
Site 3	29.0	2.3	13.3	3.6*	14.5	8.5*	8.3	2.4
20 July 1979								
Site 1	43.0	15.9*	47.7	4.3*	27.3	14.5*	13.3	1.4
Site 2	147.0	54.0*	64.0	48.7*	45.0	13.8*	15.8	10.4*
Site 3	108.0	46.7*	41.5	55.1*	20.5	15.4*	11.8	15.0*
3 August 1979								
Site 1	...	... <sup>1</sup>	57.8	13.0*	...	... <sup>1</sup>	12.5	0.7
Site 2	129.0	44.8*	105.3	11.3*	53.8	8.8*	26.8	1.8
Site 3	60.3	10.3*	60.5	1.5	32.3	6.3*	15.5	2.3

<sup>1</sup> Mean and CD not calculated because of the loss of one replicate.

and RECHER (1966) noted predation on this species by horseshoe crabs and shorebirds, respectively. Even when *G. gemma* individuals on the Cape May shore of Delaware Bay were as numerous as 206,000/m<sup>2</sup> (late spring, 1980), *L. polyphemus* contained an average of only 4.1 *G. gemma* per gut (BOTTON, 1982).

JACKSON (1968) found that *Mulinia lateralis* was ran-

domly distributed on the scale of 5 cm-by-5 cm replicates within a 0.25-m<sup>2</sup> area, and considered this a logical consequence of its reproduction by planktonic larvae. However, in the present study, the smallest *M. lateralis* individuals (those found in June, 1978) were the most aggregated. A possible explanation for the randomization in spacing among older caged clams could be movement



Table 3  
Life-history characteristics of the three principal bivalve species.

Characteristic	<i>Gemma gemma</i>	<i>Mulinia lateralis</i>	<i>Mya arenaria</i>	References
Reproductive mode	Brooder; larvae released as fully shelled embryos at 375 $\mu$ m	Planktotrophic; larvae set at 210–230 $\mu$ m	Planktotrophic; larvae set at 200 $\mu$ m	SELLMER, 1966; LOOSANOFF <i>et al.</i> , 1966
Mobility	Strong, active burrower	Active; juveniles can "hop" to avoid crowding	Limited and decreases with increasing size	BRADLEY & COOKE, 1959; VIRNSTEIN, 1977; STANLEY, 1970
Vulnerability to sediment disruption	Low; reburrowed from 5–20 cm	High	High	BRADLEY & COOKE, 1959; VIRNSTEIN, 1977
Vulnerability to predation	Low	High	High	SCHNEIDER, 1978; VIRNSTEIN, 1977; BOTTON, 1982

of individuals from sediments packed with conspecifics and *Mya arenaria*. I have no direct evidence that this occurred, although VIRNSTEIN (1977) observed that *M. lateralis* would "hop" along the substrate to avoid very densely populated areas. *M. lateralis* is a thin-shelled and shallow-burrowing clam, making it vulnerable to predation; it is a favorite prey of horseshoe crabs (BOTTON, 1982) and blue crabs (VIRNSTEIN, 1977). Predation on uncaged *M. lateralis* had an important numerical impact, but it did not equalize the spatial distribution, as might have been expected if predators were optimal patch users (HUGHES, 1980).

*Mya arenaria* is not an active burrower, and juveniles up to ~10 mm often retain a byssal attachment to sand grains (personal observations). These factors may explain the difference in spatial pattern between protected *M. arenaria* and the more active *Mulinia lateralis*. Caged *M. arenaria* individuals were generally aggregated whereas *M. lateralis* assumed a random distribution after an initially clumped set. The spatial pattern of *M. arenaria* juveniles may be maintained in larger clams in the absence of perturbations. Few *M. arenaria* survived outside cages, and horseshoe crab predation probably accounted for most of the mortality (BOTTON, 1984). The randomization of unprotected *M. arenaria* may largely be a numerical artifact, since as the mean decreases, the more likely it is that a Poisson distribution (variance = mean) is approached (CLARKE & MILNE, 1955).

This study has shown the importance of predation, disturbance, and life histories to the spatial pattern of bivalves, but several questions remain unanswered. One factor that has yet to be elucidated is the possible impact of predation and disturbance on the spatial pattern of newly set spat, *i.e.*, during the interval between settlement and "recruitment" onto a 500- $\mu$ m sieve. Secondly, aggregation was defined on the basis of replicate core samples within

a small enclosure, but if "optimal patch use" predators are operating in this system, they may be doing so on patch scales larger than those studied here. There were some large differences in Coefficient of Dispersion and/or mean number of individuals between sites separated by approximately 30 m. The cause of this variation is not known: differences may have been the manifestation of slight variations in hydrographic factors, subtle differences in the substratum, or in the case of uncaged sediments, differential mortality resulting from variations in predation and/or disturbance pressure.

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